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Observations on the behavior of some species at the edges of their ranges*

ROBERT F. GRIGGS

Various writers on ecology and plant geography have spoken of the behavior of species at the edges of their ranges—of the habitats they affect, of their reproduction, and of their abundance. These statements are of course based on impressions from the experience of the authors, but there are few extensive records of detailed observations on these matters. It is clear that a knowledge of the causes which set the limits to the distribution of species is of fundamental importance to the student of plant geography and it is obvious that the termini of the ranges are the only localities favorable to the study of these conditions. But an understanding of the matter can be reached only after the collection of a large amount of detailed evidence from numerous regions. It is with the desire of contributing one detail toward such a body of evidence that the present observations are published.

The area in which these observations were made is unusually favorable for such studies since a large proportion of the native flora here reaches its territorial limits. 122 species, about 13 per cent. of the native flora, reach, so far as is now known, the limits of their ranges in one direction or another, in the Sugar Grove region. This is a narrow strip of country covering the area of maximum outcrop of a heavy sandstone, the Black Hand Conglomerate, stretching from the edge of the terminal moraine a few miles north of the town of Sugar Grove in Fairfield County, Ohio, southward to the valley of Queer Creek, east of South Bloomingville, in Hocking County. The high cliffs and narrow ravines formed in the weathering of this sandstone impart a ruggedness to the country which is largely responsible for its botanical interest, providing suitable habitats for many of its rare plants and at the same time rendering the land unsuitable for agricultural purposes, thus in a measure insuring their preservation. It is for this reason wilder and more nearly in its aboriginal condition than the less rugged country which surrounds it. Since the time of Sullivant it has been known to the botanists of Ohio as one of the richest collecting grounds in the state. The flora of the northern portion, that lying in Fairfield County, was worked up more than seventy

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* Contribution from the Botanical Laboratory of the Ohio State University, no. 79.

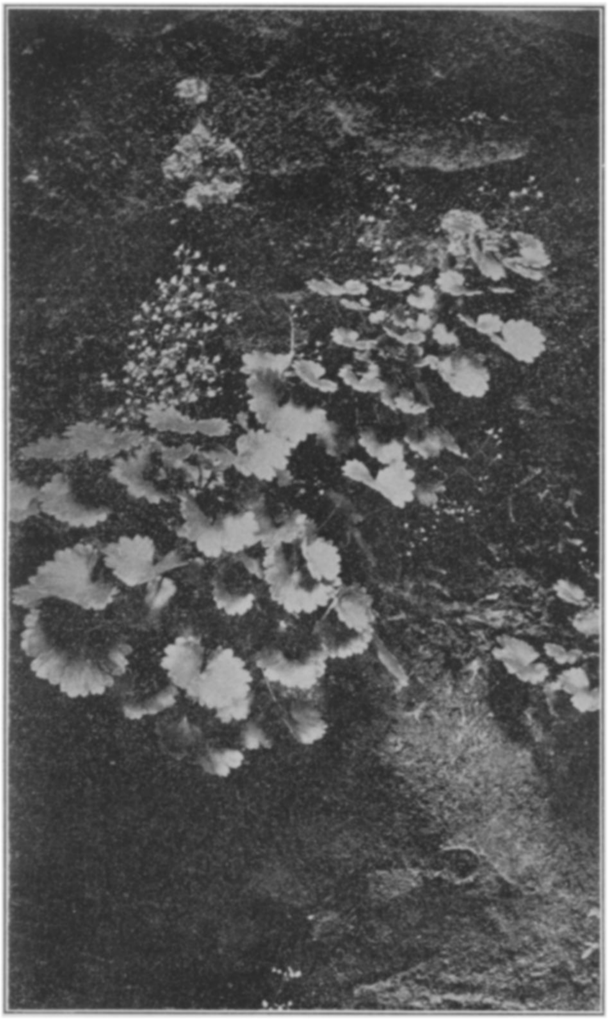

FIG. 1. *Sullivantia*, south of Sugar Grove

years ago by John M. Bigelow, an able botanist, thus affording an exceedingly interesting basis for comparison of present with past conditions.

Although the Sugar Grove area lies at the end of the long lobe of the Alleghenian Floral Area which Merriam's* map shows stretching into northeastern Ohio, the plants which terminate here are by no means all Alleghenian but include species of varied geographical affinity stretching away from the area in all directions as was shown in a preceding paper.†

It must be pointed out at the outset that the list of plants here given as reaching their territorial limits is by no means a complete or final catalogue. From the nature of the case it will be subject to a considerable amount of revision as the flora of the country becomes better known. When the manifold sources of error which enter into the study are taken into consideration the results might almost be said to have been reached by the multiplication of uncertainties. Nevertheless it is believed that present knowledge is sufficient to justify their publication for, however much the status of individual species may be changed by later discoveries, it does not seem likely that the general outlines of the account here presented will require much readjustment. The first source of error lies in the fact that as the flora becomes better known plants which are not now known beyond the borders of this area may be found in adjoining counties, thereby being removed from the list. In view of the fact that the Sugar Grove area has been more thoroughly worked than the surrounding territory the number of these may be somewhat large. Plants new to the area may be discovered and added to the list. But probably more important than changes due to either of the above causes will be the addition of numerous species, now reported from the region, whose ranges are not yet known with sufficient accuracy to enable us to tell whether they here reach their limits or not. In this category are many groups of plants which have not been collected thoroughly enough in Ohio to justify any deductions as to their distribution. Many groups are so difficult of identification that only the determinations of the specialist are dependable. These must be eliminated from consideration by plant geographers because no reliance can be placed on the various local lists which must form, in large measure, the basis of such work. Lastly there is a very large and at present increasing number of plants, the very specific identity of which is not yet understood. These include numerous recently recognized species and some older ones which have not been sufficiently studied. The difficulties occasioned by these deficiencies in our knowledge have limited the work very considerably and because of them I have sought to illustrate my points as far as possible with such well-known and conspicuous species as *Kalmia latifolia* and *Rhododendron maximum*, which are collected and listed by every amateur botanist.

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* Merriam, C. Hart. Life zones and crop zones of the United States. U. S. Dept. Agr. Biol. Survey Bull. 10. 1898.

† Griggs, Robert F. Observations on the geographical composition of the Sugar Grove Flora. Bull. Torrey Club 40: 487–499. *f. 1–10.* 10 S 1913.

The first question that arises concerning the behavior of a species at the edge of its range is as to its abundance. Do the individual plants become scarcer and scarcer until finally the species fails altogether, or is it common close up to the edge where it suddenly stops short? The species whose ranges terminate in the Sugar Grove area are therefore classified from this point of view in the following table.

ABUNDANCE OF SPECIES ON THE EDGES OF THEIR RANGES

Plants common in many stations

Andropogon virginicus
*Aralia spinosa**
Aruncus Aruncus
Ascyron hypericoides
Asplenium pinnatifidum
Aster divaricatus
*Betula lutea**
*Betula nigra**
Carex costellata
Cassia nictitans
Castanea dentata
Chimaphila maculata
Chrysosplenium americanum
*Circaea alpina**
Cornus stolonifera (abundant at Columbus at least)
Cunilla origínoides
Cypripedium acaule
Dasystoma laevigata
*Dentaria heterophylla**
Diospyros virginiana
Epigaea repens
*Eupatorium aromaticum**
Eupatorium coelestinum
*Eupatorium rotundifolium**
Fraxinus quadrangulata†
Gaultheria procumbens
Hieracium paniculatum
Hieracium venosum
Hydrangea arborescens
Isopyrum biternatum†
Juncoides saltuensis
Kalmia latifolia
Koellia incana
Lechea racemulosa
Lycopodium lucidulum
Lycopodium lucidulum porophilum
Lysimachia quadrifolia
Oxydendrum arboreum
Panicum polyanthes

Pinus rigida
Pinus virginiana
Pyrola elliptica
Quercus Prinus
Rhododendron maximum‡
Rubus odoratus
Salix amygdaloides†
Sambucus pubens
Saxifraga virginiensis
Sericocarpus asteroides
Stachys cordata
*Silene rotundifolia**
Solidago juncea
*Sullivantia Sullivantii**
Trichostema dichotomum
Tsuga canadensis
Unifolium canadense
Viola hirsutula
Viola rostrata

Common in few stations

Asplenium montanum
Azalea lutea‡
*Iris cristata**
Lobelia puberula
Pedicularis lanceolata
Phacelia dubia‡
Phlox stolonifera
Quamasia hyacinthina§
*Viola rotundifolia**

Individuals abundant in one station

Dodocatheon Meadia§ ¶
*Hypericum Drummondii**
*Melampyrum lineare**
Saxifraga pennsylvanica‡ (probably in other stations as well).

Rather common

Achroanthes unifolia
Aster macrophyllus
Anemone canadensis
Aristida dichotoma
Capnoides sempervirens
*Chrysopsis mariana**
Isotria verticillata
Lobelia leptostachys
Populus tremuloides
Porteranthus stipulatus
*Quercus minor**

Scarce

Aesculus octandra‡
Aronia nigra
*Blephariglottis peramoena**
*Lycopodium complanatum**
Lycopodium obscurum
Passiflora lutea
Pyrola rotundifolia
Scutellaria galericulata
Smilax echirrata
Valeriana pauciflora§
Viburnum dentatum
Viburnum molle.

Individual plants rare and widely scattered

Afzelia macrophylla
Asclepias Sullivantii
Asclepias variegata
Blephariglottis lacera
Fraxinus nigra||
Gentiana crinita
Gymnocladus dioica§ || **
Lycopodium clavatum
Napaea dioica
Parnassia caroliniana
Psoralea Onobrychis
Stylosanthes biflora

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* Species confined to the southern portion of the area.

† Species reaching their limits immediately to the west of the area.

‡ Species confined to the northern portion of the area.

§ Main body of range ends in Central Ohio but extends locally into Pennsylvania.

¶ Also reported from another station by Bigelow.

|| Not known south of Columbus

** Fairly common a few miles to the westward.

Frequency of occurrence not observed

Bidens aristosa
Eatonia nitida
Panicum stipitatum
Panicularia elongata
Rynchospora glomerata
Solidago erecta

Plants reported by Bigelow[*] but not now known in the area

Brauneria purpurea.§
Cardamine rotundifolia
Carduus virginicus
Cypripedium Reginae
Dasyphora fruticosa
Lysias orbiculata
Panicularia acutiflora
Panicularia pallida
Trifolium reflexum
Trollius laxus
Veratrum Woodii

SUMMARY

Common in many stations	58
Common in few stations	9
Individuals abundant in one station	4
Rather common	11
Scarce	12
Rare	12
Frequency of occurrence not observed	6
Not now known from the area	11
Total	123

It is clear from these lists that in this region the species in which the individuals become scarcer and scarcer until it fails altogether is exceptional. In the majority the individuals are abundant in their respective stations up to the very edge of their ranges.

But one who studies the ranges of species in a broad way rather than in a restricted area, gets a decided impression that the ranges of most species are bordered by a fringe of outlying stations at considerable distances from each other. Many of the most interesting species of the Sugar Grove region are such outliers. Those which are not known elsewhere within approximately one hundred miles are listed below. It may be asserted with some confidence that some of these such as the *Rhododendron* and the *Azalea* really do not occur elsewhere within the boundaries of the state of Ohio, but some of the others have not yet been searched for enough to justify much confidence in their assignment to this category. One of the list, *Silene rotundifolia,* occurs in Jackson County only twenty-five miles south of our area but as its next known station is far beyond the borders of the state, it seems only proper to include it here. Numerous other species must be outliers separated from their nearest stations by smaller intervals, but the distribution of the Ohio flora is not yet well enough known to enable us to pick out these species with sufficient accuracy to justify the attempt. The list of outliers separated by the larger interval includes:

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[*] Florula Lancastriensis. Proc. Medical Convention of Ohio 1841: 49–79. Columbus, 1842.

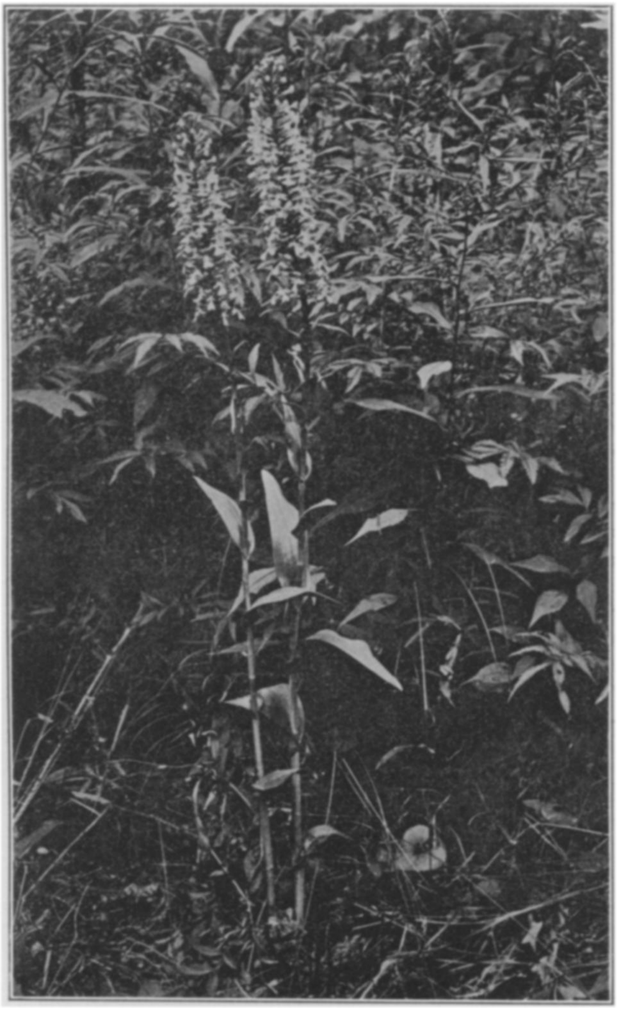

FIG. 2. *Blephariglottis peramoena* in flower at Sugar Grove. Plant unusually strong, with unusually large flower clusters.

Species	Next known station
Achroanthes unifolia	Only Ohio Station.
Aralia spinosa	Clermont Co.
Asclepias Sullivantii	Erie Co.
Asclepias variegata	Summit Co.
Asplenium montanum	Summit Co.
Azalea lutea	Only Ohio Station.
Betula lutea	Wayne Co.
Circaea alpina	Clarke Co. (75 miles) and Summit Co.
Cypripedium acaule	Said formerly to have occurred in Licking Co. immediately to the north.* Nearest station known to me, Medina Co.
Dodecatheon Meadia	Clarke Co. (75 miles).
Eupatorium aromaticum	Only Ohio Station.
Eupatorium rotundifolia	Only Ohio Station.
Hypericum Drummondii	Clermont and Ashtabula Counties.
Lycopodum clavatum	Geauga Co.
Juncoides saltuensis	Mahoning Co.
Melampyrum lineare	Lorain Co.
Phacelia dubia	Only Ohio Station.
Phlox stolonifera	Only Ohio Station.
Pyrola rotundifolia	Summit Co.
Polygonum arifolium	Wayne Co.
Rhododendron maximum	Only Ohio Station.
Silene rotundifolia	Hocking and Jackson Counties only.
Sullivantia Sullivantii	Highland Co.
Viola hirsutula	Only Ohio Station yet known.
Viola rotundifolia	Cuyahoga Co.

There are on the other hand many species which are abundant all along the edges of their ranges. The plants in this category contrast strongly with the outliers, which are plants of diverse geographical affinity, in that they belong for the most part to two definite groups: Alleghenian plants here on the western edges of their ranges, and southern plants limited to the poor soils of the uplands. Some of them, such as *Pinus rigida*, are to be found within a few miles almost anywhere that one may choose to enter their ranges, even though the individuals may be somewhat scarce at the very edge. In some of the others the case is not so clear from collections at present available, but all those here included are known from at least three contiguous counties in our region. They are moreover plants which field experience leads me to

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* Jones, H. L. Flora of Licking Co. Bull. Sci. Lab. Dennison University **7**: 85. 1892.

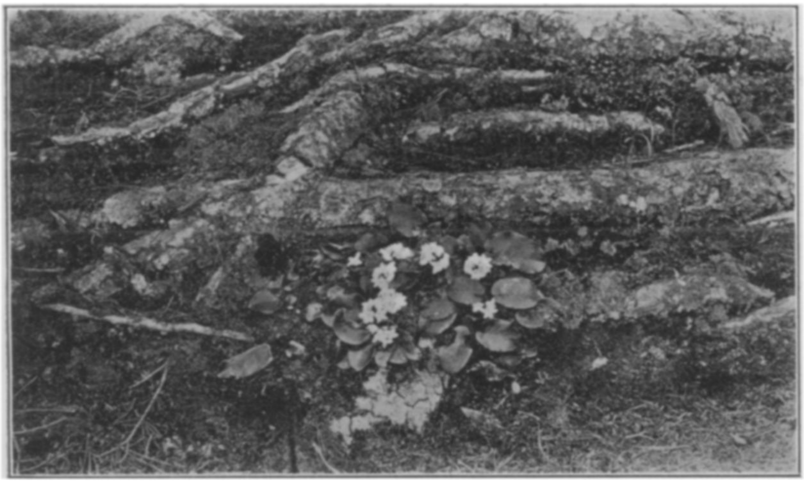

FIG. 3. A small plant of *Epigaea repens* in flower at Sugar Grove

suppose common over much wider areas than is shown by the collections. This list includes:

Andropogon virginicus
Asplenium pinnatifidum
Aster divaricatis
Aruncus Aruncus
Ascyron multicaule
Betula nigra
Castanea dentata
Chimaphila maculata
Cunilla originoides
Daystoma laevigata
Epigaea repens
Eupatorium coelestinum
Gaultheria procumbens
Gyrostachys gracilis
Hieracium venosum
Kalmia latifolia
Lycopodium lucidulum
Lycopodium complanatum
Oxydendrum arboreum
Pinus rigida
Pinus virginiana
Pyrola elliptica
Quercus Prinus
Saxifraga virginiensis
Sericocarpus asteroides
Solidago bicolor
Tsuga canadensis

If now we attempt to determine by analysis the factors which cause the termination of the ranges, our first inquiry is naturally concerning the reproductive functions of the plants under discussion. It has been supposed, somewhat generally, that the reproductive functions of many species fail at the northern or southern edges of their ranges. The failure may occur at any one of several points in the cycle: a plant may not produce flowers in sufficient numbers to maintain its place in plant society; it may flower freely but fruit sparingly either because of faulty fertilization or because of a short season; conditions while adequate for adult plants may be unfavorable for the development of seedlings. To determine how far these various possibilities restrict the spread of the plants under consideration they have been classified according to the apparent success of the reproductive system as follows:

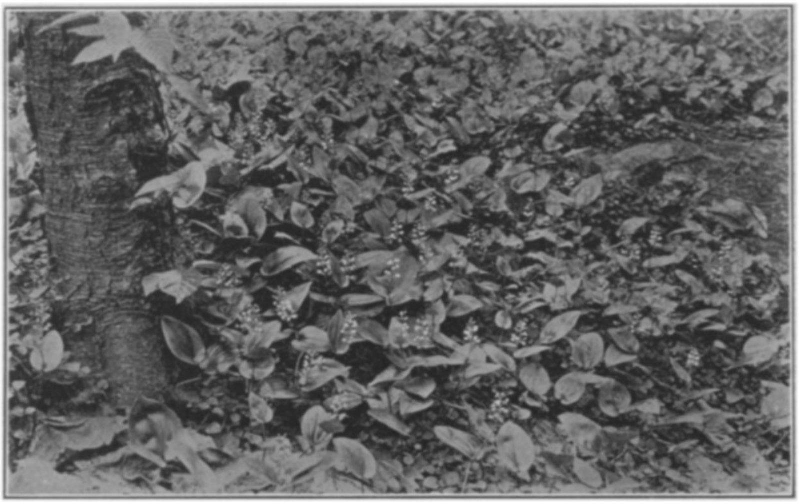

FIG. 4. *Unifolium canadense* at Sugar Grove. Beds as thick as this are rare in this region. Although flowering freely, the plant does not fruit well

Reproduction of species on the edges of their ranges

Flowering scantily

Gaultheria procumbens[*]
Isotria verticillata
Passiflora lutea
Phlox stolonifera[*†]
Pyrola elliptica[*]
Pyrola rotundifolia[*]
Sambucus pubens[*†]
Stylosanthes biflora

Fruiting sparingly although flowering freely

Aesculus octandra[‡]
Asclepias variegata
Blephariglottis lacera
Diospyros virginiana
Lycopodium lucidulum porophilum[§]
Lysimachia quadrifolia
Napaea dioica[¶]
Quercus minor
Rubus odoratus.
Unifolium canadense

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[*] Fruit appears to "set" and mature well.

[†] Species confined to the southern portion of the area.

[‡] Species confined to the northern portion of the area.

[§] Sporangia comparatively scarce.

[¶] Dioecious, only one plant found.

Flowering freely, fruiting not observed

Achroanthes unifolia
Anemone canadensis
Aronia nigra
Aster macrophyllus
Bidens aristosa
Blephariglottis peramoena†
Chrysopsis mariana†
Chrysosplenium americanum
Dentaria heterophylla‡
Eatonia nitida
Epigaea repens
Hypericum Drummondii† ||
Isopyrum biternatum¶
Iris cristata†
Polygonum arifolium†
Quamasia hyacinthina¶
Scutellaria galericulata
Solidago erecta
Solidago juncea
Stachys cordata
Trichostema dichotomum
Valeriana pauciflora§

Fruiting freely

Afzelia macrophylla
Andropogon virginicus
Aruncus Aruncus
Ascyron multicaule
Azalea lutea
Capnoides sempervirens
Carex costellata
Castanea dentata
Cunilla originoides
Cypripedium acaule°
Dasystoma laevigata
Epigaea repens
Dodecatheon Meadia† **
Eupatorium aromaticum†
Eupatorium coelestinum
Eupatorium rotundifolium†
Hieracium paniculatum
Hydrangea arborescens
Koellia incana
Juncoides saltuensis
Lobelia puberula†
Lycopodium lucidulum††
Lycopodium clavatum † ††
Lycopodium complanatum † ††
Lycopodium obscurum† ††
Panicum polyanthes
Panicum stipitatum
Pedicularis lanceolata
Phacelia dubia‡
Porteranthus stipulatus
Salix amygdaloides¶
Sericocarpus asteroides
Viola hirsutula
Viola rotundifolia†
Viola rostrata

Fruiting freely, seedlings also abundant

Aralia spinosa†
Aster divaricatus
Betula lutea†
Betula nigra†
Cassia nictitans
Circaea alpina†
Gymnocladus dioica§ ¶
Hieracium venosum
Kalmia latifolia
Melampyrum lineare†
Oxydendrum arboreum
Pinus rigida
Pinus virginiana
Quercus Prinus
Rhododendron maximum
Saxifraga pennsylvanica‡
Saxifraga virginiensis
Silene rotundifolia†
Sullivantia Sullivantii†
Tsuga canadensis

|| Not maintaining itself, perhaps only a waif.

¶ Species reaching their limits immediately to the west of the area.

° Many flowers are unfertilized but fruit is common.

** Also reported from another station by Bigelow.

†† Sporangia abundant.

Pteridophytes, prothallia not observed

Asplenium montanum
Asplenium pinnatifidum
Lycopodium clavatum†
Lycopodium complanatum†
Lycopodium lucidulum
Lycopodium lucidulum porophilum
Lycopodium obscurum

Species abundant by vegetative propagation (scattered through above groups)

Cypripedium acaule
Gaultheria procumbens
Iris cristata
Lycopodium lucidulum
Lycopodium lucidulum porophilum
Phlox stolonifera†
Unifolium canadense

Fruiting yet to be observed

Aristida dichotoma
Asclepias Sullivantii
Cornus stolonifera
Fraxinus nigra
Fraxinus quadrangulata
Gentiana crinita
Lechea racemulosa
Lobelia leptostachys
Panicularia elongata
Parnassia caroliniana
Populus tremuloides
Psoralea Onobrychis
Rynchospora glomerata
Smilax ecirrhata

SUMMARY

Flowering scantily	8
Fruiting sparingly although flowering freely	10
Flowering freely, fruiting not observed	22
Fruiting freely	35
Fruiting freely, seedlings abundant	20
Pteridophytes, prothallia not observed	7
Abundant by vegetative propagation, species scattered through the above groups	7
Unobserved 14+11,	25
Total	134
Duplications	12
Net total	122

Such a classification to be of the maximum value should have been made by one familiar with the various species throughout the whole extent of their ranges. Species that appear to the writer to fruit abundantly may fruit so much more abundantly in other regions that their fruit in the Sugar Grove area would be scarce by comparison. The wintergreen, *Gaultheria procumbens*, is a case in point. The berries are apparently sufficiently common to supply enough seed for the perpetuation of the species, and the plant would accordingly have been classed as fruiting freely but for the acquaintance of the writer with the same species in New England where the berries are borne in such great profusion—six or seven to a stalk—as to make the Ohio plants bearing rarely more than one or two berries and those only on about one plant in ten, seem sterile by comparison. On the other hand some species flower sparingly throughout their range so that similar behavior at the termini would not be unusual. In making the tables I have classed as fruiting freely all those species whose seed production appeared adequate for their perpetuation.

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† Species confined to the southern portion of the area.

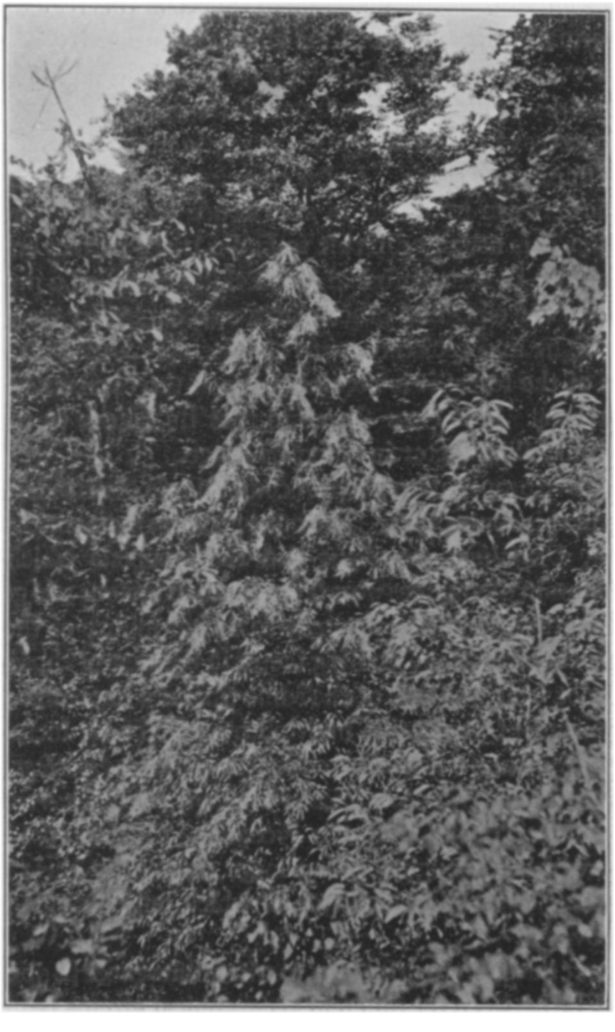

FIG. 5. *Oxydendrum arboreum* in fruit at Sugar Grove

But allowing for all the changes which might be made in the classification by one of wider field experience than the writer, it seems certain that failure of the reproductive functions is an unimportant factor in the termination of ranges in this region. Most plants normally produce such an enormous quantity of surplus seed that even a considerable falling off in seed production would not necessarily affect the abundance of the species.

The success of the seedlings is apparently much more important than the number of seeds. *Rubus odoratus* is a case in point. Although flowers are produced in abundance the fruit does not set well so that it is usually difficult to find a berry perfect enough to be palatable. In the aboriginal forest this species led a precarious existence on the cliffs and other places unoccupied by trees, where sufficient light and moisture were obtainable. But with the destruction of the forest it is becoming one of the commonest plants of the ravines. It is clear therefore that its failure to fruit well is not a controlling factor in fixing its range.

Vegetative propagation plays of course a role of considerable importance in this connection. The most striking instances are *Phlox stolonifera*, *Unifolium canadense* and the lycopods which would hardly maintain themselves were it not for their stolons and gemmae.

On the other hand it seems safe to assign failure of the reproductive mechanism as the limiting factor in the case of those species which do not fruit well and at the same time are uncommon, being without means of vegetative multiplication. These include only *Asclepias Sullivantii*, *Aseculus octandra*, *Asclepias variegata*, *Blephariglottis lacera*, *Napaea dioica*, *Passiflora lutea*, *Quercus minor* (?), *Stylosanthes biflora* and the lycopods, *L. obscurum* and *L. clavatum*, which although forming large masses by their runners are yet scarce, especially the latter, of which only a single bed has been discovered.

The next question to arise is as to what differences in abundance there may be between the different geographical groups represented in the lists. What differences are there between northern and southern or eastern and western plants? A comparison of the lists given above with those presented in the preceding paper* gives the data shown in tabular form below.

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* Griggs, Robert F. Observations on the geographical composition of the Sugar Grove flora. Bull. Torrey Club 40: 487–499. *f. 1–10.* 10 S 1913.

	Common	Common Few Stations	Abundant One Station	Rather Common	Per Cent. Common	Scarce	Rare	Per Cent. Uncommon	Unobserved	Flower Scantily	Fruit Sparingly	Per Cent. Not Fruiting Well	Flower Freely	Fruit Freely	Seedlings Abundant	Per Cent. Fruiting Well	Not Observed	Total
Alleghenian.....	18	0	1	4	65	4	4	22	7	5	5	28	6	9	5	53	9	39
New England Appalachian..	11	1	0	0	80	0	0	0	2	0	0	0	1	6	6	93	1	14
Appalachian....	7	4	0	0	92	0	0	0	1	1	0	8	1	4	3	66	3	12
Carolinian......	16	2	0	5	68	2	3	15	4	2	4	18	6	11	3	61	6	32
Western.......	3	1	2	0	40	3	4	47	3	0	1	7	5	2	2	60	5	15
Northern......	2	1	2	2	77	1	0	11	1	0	0	0	3	2	1	66	3	9

This table does not indicate that in this region species behave differently on different edges of their ranges. Except in one case the differences shown are too small to be significant in view of the small numbers involved. The abundance and reproduction of species terminating in this area are evidently matters concerned with the individual peculiarities of the particular species rather than with its geographical position. The large number of rare plants among those from the west is, however, very striking. When this is coupled with the fact that a large proportion of them are known from scattered stations far to the eastward of their main range, it becomes significant.

There is a widely held idea, which owes its origin I believe to Blytt* though it may be much older, that, whereas a species may be ubiquitous in the center of its range, occurring in all sorts of habitats because highly favored by climate, at its areal limits it will be closely limited to those conditions which are most favorable to it. According to this reasoning we should be best able to determine the conditions most favorable to any given species by observing its behavior on the edges of its range. The theory is so plausible that one would like to accept it and apply it to our plants. But unfortunately certain of our Sugar Grove plants do not seem to behave according to expectations and raise doubts concerning its validity.

The chestnut is one of the most typical of all the "calcifuge" plants and its distribution in central Ohio fulfils expectations in this regard. It is absent from the limestone country about Columbus but appears immediately as one enters the outcrops of sandstone about twenty miles to the eastward. From this point it is abundant all over the sandstone part of the state and is one of the most important timber trees about Sugar Grove. What was my surprise then, on mapping its general range, to find its Michigan stations described in these terms by Beal:* "Occurs abundantly

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* I am unable to find the reference to Blytt's paper; see also Cowles, Physiographic Ecology of Chicago and Vicinity. Bot. Gaz. 31: 83. 1901.

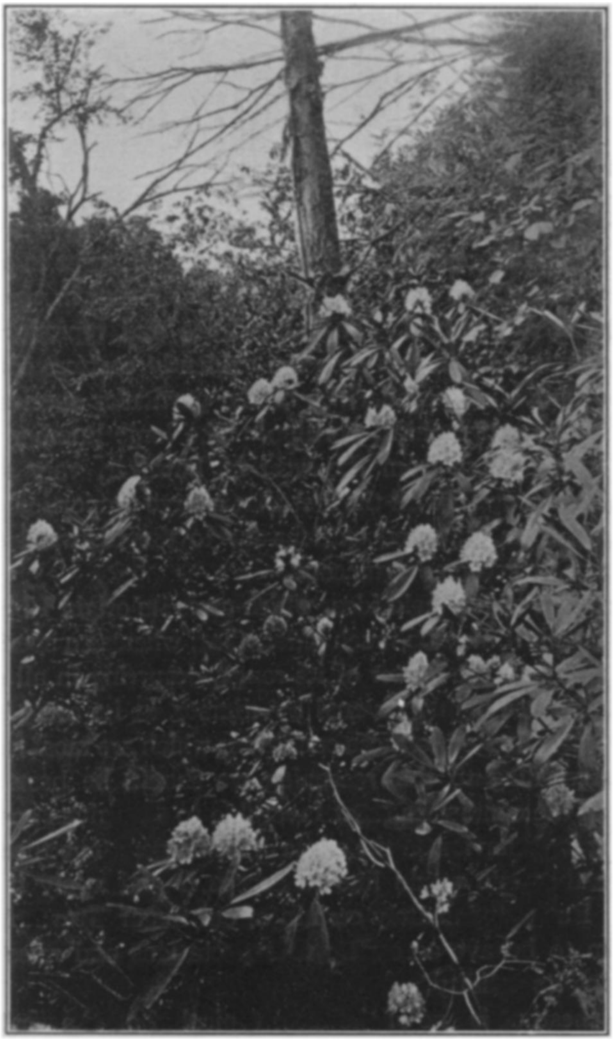

FIG. 6. *Rhododendron* at Sugar Grove. (Photograph by J. E. Hyde.)

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* Beal, W. J. Michigan Flora 69. Lansing, 1904.

along an outcrop of Helderberg limestone in E. Monroe Co. and Wayne Co., C. F. Wheeler." Thus its preferences in one part of the edge of its range would make it a calciphile and in another part a calcifuge plant.

Rhododendron maximum is interesting in this connection. Its typical habitat is the densest shade in deep forests, where it forms impenetrable thickets. This for the most part is its habitat in the Sugar Grove area where it is found at the base of the cliffs in deep ravines on slopes with a northern exposure. In the northern section of the area immediately around Sugar Grove I have never seen it except in such situations. But in the southern section although likely habitats are common enough it is absent except for two isolated patches of small extent. One of these is near "Written Rock" on Clear Creek and the other is at the head of Laurel Run. In both of these stations the plant grows and apparently thrives measurably well as a crevice plant high up *on cliffs with extreme southern exposure* in conditions far different from its supposed optimum.

Aralia spinosa was almost exclusively a crevice plant in the primeval forest, occurring high up on the faces of the cliffs and dropping its seeds into the caves below where they sometimes took root, as in Old Man's Cave. Since the timber of the higher slopes has been cut off, the plant has multiplied extraordinarily until it has become a common pest on lumbered hillsides. The manuals credit it with growing in "Damp moist soil in the neighborhood of streams." But in the valley of Queer Creek only a single specimen and that dead, was found in the moist bottom land. Mohr* describes its habitat in Alabama as "Damp borders of woods and copses." Hilgard,† page 495, describes it as a lowland plant in highly productive calcareous soil and again, on page 515, states that with the *Liriodendron*, black walnut, Kentucky coffee tree, and others which are like it normally lowland plants, it may ascend in calcareous regions into the uplands as well. The rock in whose crevices it occurs in our area is not limestone but a pure sandstone which is sometimes quarried for glass sand; the hillsides which it has invaded are very poor land which was originally covered by a mixed forest of scrub and pitch pine, black oak and blueberries. Through the whole region much of the land has been abandoned and not more than half of the houses are now occupied. The crevices in exposed rocks are the poorest of all the habitats in the region and it can be shown that the majority of the chasmophytes are plants which have been crowded out of the more favorable habitats which they would quickly repopulate, as the *Aralia* has done, were their more successful neighbors removed. This very plant indeed, when the forest is removed, gives abundant evidence of the kind of habitat it prefers. It is really a *sun-loving* plant and grows only where sunlight is abundant. In the primeval forest the upper faces of the cliffs were the only situations in which a plentitude of light was available to a plant of such humble stature, so here it developed wherever together with sunlight sufficient water was present.

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* Mohr, Charles. Plant Life of Alabama. Cont. Nat. Herb. **6**: 640. 1901.

† Hilgard, E. W. Soils. Macmillan Co., 1904.

Even so few examples as these are sufficient to destroy the utility of the theory that at the edges of their ranges, species are confined to the most favorable habitats. Where it describes conditions previously known to obtain, well and good. But it cannot be generalized nor can it serve as a guide to the optimum habitats of plants whose preferences in this matter are unknown. Like much *a priori* reasoning it presents a conclusion which may be true rather than one which must be true. Moreover, another line of *a priori* reasoning might in this case lead us to diametrically opposite conclusions. In the center of its range a plant, being supposedly favored by all the conditions of its environment, is able to compete with other plants at an advantage and maintain a place for itself in various habitats. On its areal limits on the other hand environmental conditions are supposedly less favorable to this species than to others with which it will therefore be compelled to compete at a disadvantage. This may be brought about either by unfavorable physical conditions such as soil, climate, etc., or by the entry into the struggle for place of species absent from the center of the range which have an advantage over the given species in rapidity of growth or the like. The species in question is therefore driven out of the most favorable habitats and must find a place for itself where it can. This is exactly the situation of *Aralia spinosa* which in the dense forest that originally covered the Sugar Grove region could grow only on the cliffs, where the successful forest trees could neither follow it nor deprive it of its light.

We seem, therefore, to have made little progress in the effort to determine the causes of the termination of ranges. The feeling that it was not caused by such factors as I could observe has also been borne in upon me as I have repeatedly studied the plants in the field. It has been quite impossible to imagine why a given species should be abundant in one valley and absent from the next one only a few miles away when all conditions seemed similar.

It is generally supposed that climatic influences are the most important factors in determining plant ranges. By appropriate manipulation of climatic data it is possible to draw striking parallels with vegetational zones. Thus Merriam* has constructed maps from temperature data which conform remarkably closely to the life zones of North America. Transeau† likewise by plotting the ratio of evaporation to rainfall has made a map conforming to the forest areas of eastern North America in scarcely less striking fashion. Although dealing with factors to a large extent unrelated to each other, the correspondence of each of these maps with biogeography is so striking as to lead almost irresistibly to the conclusion that each of them represents the causative factor. They are, however, admittedly made to fit the facts of distribution and have not the weight that they would possess if constructed *a priori* by someone unfamiliar with the biogeography of North America. Moreover, it is not possible to state with any confidence the climatic requirements of any given species.

If climate were the principal factor restricting the spread of plants the edges of their ranges should exhibit one of two conditions: (1) Since climate changes vary gradually from place to place the controlling conditions should appear very gradually and the plants in response finding the conditions of life more and more difficult should become scarcer and scarcer and finally fail. This, however, happens comparatively seldom in this region. (2) The range should be fringed with outliers occupying habitats where the climatic conditions were locally favorable. This is undoubtedly frequently the case. Bessey's* finding *Adiantum Capillus-veneris* near a hot spring in South Dakota is a notable example. The presence of *Betula lutea* and some other northern plants in the deep cold ravines of the present area may be set down rather confidently as a local instance. I would not dare, however, to apply this explanation to more than seven of the twenty-five outliers listed above; for the others it seems clearly out of the question.

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* Merriam, C. Hart. Laws of temperature control of the geographic distribution of terrestrial plants and animals. Nat. Geogr. Mag. **6**: 229–238. 1894.

† Transeau, E. N. Forest centers of eastern America. Am. Nat. **39**: 875–889. 1905.

For many of the plants which terminate here, especially those which I know best because their boundaries cross the area, it is quite beyond my power of analysis to discover any reason why they should find their limits where they do and not go a few miles further. The easiest explanation of my inability to fix upon the reason for the location of their termini is that there is no reason; that they do not occupy ranges fixed by climatic conditions but are in process of adjustment. Observation of these plants seems to indicate that competition with other plant species is more important than climate in fixing the limits of their ranges. The case may be best presented by a few concrete examples:

Silene rotundifolia is common in the crevices of rocks regardless of exposure (not on "shaded banks") throughout the southern section of our area whence it extends southward along the western slope of the mountains to Tennessee. It is common up to "Cantwell Cliffs" but here it suddenly stops and has never been found further north. Suitable habitats, however, are by no means lacking.

Aralia spinosa is another plant of this sort. This species is of such a character that he who travels the brush, whether he be botanist or not, is forcibly made aware of its presence wherever it grows. It is a common plant over most of the southern states reaching its northern limits in southern Illinois, the Sugar Grove area, and Pennsylvania. It is abundant in the valley of Queer Creek and in some places on Big Pine Creek, occurring on the higher slopes where the timber has been cut off. As already indicated its place in plant society has been greatly enlarged by the lumberman so that it is now much more common than formerly and its seedlings are taking possession of many cut-over woods. But its terminus is perfectly sharp; not a single individual has been found further northward, although a constant lookout has been kept for it. The increase in available habitats is giving it a continuous range, whereas formerly it occupied only isolated stations in the crevices like *Silene rotundifolia.* This change greatly increases the chances of successful reproduction and the plant gives every evidence of spreading northward. But like *Silene* it has no special means of seed dispersal and its progress is very slow.

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* Bessey, C. E. One thousand miles for a fern. Asa Gray Bull. 8: 2–6. 1900.

A large proportion of the western plants terminating here behave similarly. *Afzelia macrophylla,* for example, is rare in our area having been seen only once by the writer but under circumstances which clearly indicate its powers of invasion, for its seedlings were more than holding their own against the former occupants of the soil. The eastern edge of the range of these species consists of a circle of such outliers located where chance seeds have dropped in advance of the range. The large proportion of western plants which are rare with us and at the same time are known far beyond our area may indicate that these are not merely characteristics of the individual species but that there is a somewhat systematic migration of western plants eastward.

The converse of the same proposition is presented by such a plant as the hemlock, *Tsuga canadensis.* The main body of its range ends in the Sugar Grove region, where it is common, especially in the deepest canyons. It occurs in numerous outlying stations, however, far to the west and south. One of these is in the mountains of western Alabama;* another is on the Green River in Kentucky; a third,† which is better known, is near Greencastle, Indiana, where it occurs together with the yew on a limestone soil. Since it is usually found on rocks one might suppose that the causes of its termination were physiographic—the absence of suitable habitats in the intervening country. But although most often found on rocks, both sandstone and limestone, it is by no means a chasmophyte by preference but is at its best in the richest of deep alluvial bottomland soils as in the canyon of Queer Creek in the southern section of the present area. In the northern section of the area, however, where the valleys are somewhat older in a physiographic sense, the hemlock is restricted to the rocks around the edges of the ravines while the bottom is occupied by a mixed *Liriodendron* forest. A study of the plant societies here has convinced me, however, that it once occupied the bottoms as it still does in the more inaccessible valleys further south, but that it has been driven out of the more favorable habitats by the hardwoods. It seems probable that it once ranged continously over all of Ohio and Indiana but that it has been displaced except in a few outlying rocky stations where it has been able to maintain itself till the present time. Study of the reproduction of the hemlock forest in the present area would indicate moreover that under present conditions, as modified by man, it will soon disappear from these stations as it has from the surrounding territory. On account of the superficial root-system, seedlings are unable to get a start except in very humid conditions such as obtained in the virgin forest. Wherever the humidity has been lowered by clearing, the hemlock seedlings are quickly dried out and killed both on rocks and in the bottom, while the hardwood trees which spring up beside them thrive where the soil is sufficiently deep.

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* Mohr, C. Plant Life of Alabama. Cont. Nat. Herb. **6**: 34. 1901.

† Coulter, Stanley. Indiana Geol. Surv. Rep. **24**: 616. 1899. Since this paper was in type I have found that is by no means the only station in Indiana as is stated by Coulter.

The reasons for the increased abundance of such a plant as *Aralia spinosa* are of course not natural but artificial, introduced by the advent of man. On first thought one might be inclined to rule out such cases, but clearing and cultivation of the land make little if any change in climatic conditions. Their effect is in changing the conditions of competition between plant species. How profound this influence has been is forcibly brought to our attention every day by our pestiferous weeds, many of which are native species originally present in the forests but in insignificant numbers. All of these are species with some effective means of seed dispersal and their conquest of the country is now so complete that it is impossible to imagine their aboriginal condition. It is only the slow-moving species whose progress can be now studied.

That plant competition often plays a larger part than climatic influences is also indicated by the fact that most plants thrive and successfully reproduce when planted under conditions widely different from those of their natural habitats if only competing plants are removed. Professor J. H. Schaffner informs me that *Cactus missouriensis* in Kansas at the eastern edge of its range is confined to the dry tops of the hills where nothing else can grow. But when he transplanted it to a rich shaded yard it grew far more rapidly than before and attained twice the size of wild specimens as long as grass was kept away from it.

The case of the hemlock is a good illustratiom of one very important factor which has not been touched on—the historical factor.* The reasons that the hemlock occupies its present range are primarily historical. It is here because this particular species and not some other analogous conifer like the Norway spruce was present in eastern North America during the Glacial Period and because it has not yet been completely displaced by the post-glacial flora. It occupies the canyon of Queer Creek not because it is better suited for that situation than any other plant of the region but simply because the invading hardwood forest has not had so good an opportunity to gain a foothold there as elsewhere.

There are thus apparently *tension zones* between different species somewhat similar to the familiar tension zones between plant societies. These zones are as critical in the study of plant geography as are formational tension zones in ecology. For in these zones it can be seen that some species are advancing while others are being beaten back. Just as one can determine the course of ecological succession from the behavior of plant societies in the tension zones so one can determine the trend of geographical movements† by a study of the tension zones at the edge of plant ranges.

And yet there can be no doubt that climatic conditions are of fundamental importance in determining the ranges of plants. It is apparent that plants tend to spread and would finally come to occupy ranges as large as their adaptability to climate would permit, just as stream erosion would reduce all regions to base-level. Under such conditions competition between species would cease to be a factor, for that battle would have been finished and the weaker species eliminated. With competition would disappear the historical factor which is largely a record of the state of the struggle.

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* For a discussion of the importance of the historical factor, see Adams, C. C. The Postglacial dispersal of North American Biota. Biol. Bull. **9**: 53–71. 1905.

† Adams (Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull. **3**: 115–131. 1902) has insisted that biogeography must be put on a dynamic basis. Bessey, C. E. (Plant migration studies. Univ. Neb. Studies **5**: 11–27. 1905) has shown that the forest trees are invading Nebraska from all sides, largely on account of the elimination of prairie fires.

At best, however, such conditions obtain only for part of the plants. There are always a large number of species like the cactus cited above which are driven out of the favorable habitats by more aggressive plants but find a place in unfavorable stiuations where their competitors cannot follow them but which they can endure. Thus the plants of favorable habitats may be limited by climatic factors while those of unfavorable are largely controlled by competition. Accordingly one may find a species dominant at one edge of its range but outcast at the other. As one passes from zone to zone into more and more severe conditions he may find the outcast plants of one region becoming the dominant ones of the next, giving an appearance of complete adjustment to climatic conditions whereas in reality only half the vegetation is controlled by climate.

Where conditions have remained stable such adjustment should be found everywhere but as species approach the limits of their adaptability to climatic conditions their progress may be expected to be increasingly retarded so that as in base-leveling the last stages of the process are exceedingly slow. With our present limited knowledge of plant ranges it would be rash to suppose that complete climatic adjustment of vegetation is as rare as the completion of a cycle of erosion, but it is evident that various factors may intervene to disturb the process before completion. (1) The minor changes brought about by shifting physiography might affect the distribution of such plants as require certain peculiar habits. (2) Whenever and wherever new types of plants, or of animals that feed upon them, are evolved, their entry into the struggle for existence introduces an entirely different set of conditions and throws the whole vegetation* out of adjustment.

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* Shreve in a paper entitled "The rôle of winter temperatures in determining the distribution of plants," read before the Botanical Society of America at Atlanta,

Changes of this character in the past are responsible for profound modifications of present phytogeography, such as the extinction of many types of conifers in the northern hemisphere. There is no reason for supposing that evolution has ceased or that its progress is so slow as to make its effect on plant competition unobservable. (3) We know very little about the rapidity of climatic changes but climatic revolutions in the past have wrought great changes in vegetation. It is hardly reasonable to suppose that such changes are not still going forward. It may be doubtful, perhaps, whether they are rapid enough to be discernible in the present day flora, but it is clear that exceedingly slow movements of vegetation may be readily detected by observations of the tension zones between the ranges.

Broad conclusions involving a systematic shifting of plant ranges cannot of course be drawn from study of a single area. But the behavior of the species reaching the edges of their ranges in the Sugar Grove area seems to indicate very clearly that the ranges terminating there are not fixed but are changing. Plants of boreal affinity are apparently being displaced by others from the west and south. This obviously falls into line with the biotic changes which are known to have occurred since the glacial period. The conditions of the tension zones between the species terminating at Sugar Grove find, therefore, their most rational interpretation as a present-day continuation of the floristic movements following the glacial period.

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31 D 1913, reported that the northward and altitudinal extension of the lowland flora in the vicinity of the Desert Botanical Laboratory is checked by winter temperatures. This would of course fall into line with other facts, such as extremely localized ranges and the rich development of endemic forms, which indicate for the flora of the southwest a great age as compared with the comparative youth of the flora of the northeastern states.